• Physiology and Biochemistry of • Abscission in the Cotton Plant

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SUMMARY

This bulletin summarizes the critical research conducted during the past 70 years on the abscission problem of shedding and defoliation in cotton.

The basic cause of abscission in cotton is still unknown, although there is much evidence in the literature regarding the specific role of many individual factors in the process. After reviewing and evaluating the factors known to affect the loss of fruiting forms and leaves in the cotton plant, it is concluded that abscission must be considered in light of an interaction of many diverse factors. Any attempt to explain such a complicated process as abscission in terms of a single factor has proved to be unsuccessful. Until the key block in the normal metabolic pathway that initiates the train of events that are eventually consummated in the shedding of fruiting forms or leaves is known, little hope exists in solving or controlling abscission in cotton.

Regardless of the best varieties and cultural methods of production used, the cotton plant usually matures bolls from only about 40 percent of its squares. This has led many research workers to conclude that shedding is an inborn, unalterable, protective mechanism which maintains the proper vegetative-fruiting balance in response to the environment. Although cotton already is an efficient plant in terms of the percentage of its total dry weight that goes into boll production, the above conclusion ignores entirely valid evidence that still greater fruiting efficiency is possible. Often when squares and bolls are shedding in waves, there are ample nutrients and food reserves in the plant to support them. Also, the shed squares or young bolls represent wasted nitrogen and energy sources in the overall economy of the plant. With the availability of new techniques and research tools, fresh approaches to the problem of shedding, some of which have been pointed out in this bulletin, should be investigated. New shedding studies are justified on both theoretical and practical bases. It is highly unlikely that practical control of shedding in cotton will be achieved until the basic cause or causes are known.

Except for minor differences in susceptibility to abscission and in the pattern and rate of the process, there are no valid reasons to believe that the basic cause or causes of shedding and defoliation in cotton are different. Little is known of concrete nature regarding the specific enzyme systems involved in abscission or how they interact with promoting and inhibiting factors. Progress in understanding the basic mechanism of abscission in cotton and why it differs from other species, as well as the devising of practical methods to control abscission, will be seriously retarded until this knowledge becomes available.

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Physiology and Biochemistry of Abscission in the Cotton Plant

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THE DETACHMENT OF ORGANS OR PLANT PARTS constitutes the abscission process. Although the sloughing of bark and other parts, the dehiscence of fruits, defoliation and the loss of fruiting forms all take place in the cotton plant, our knowledge of these processes is restricted mostly to the latter two aspects mainly because of their fundamental and practical importance to cotton culture. This report will be confined to defoliation and shedding. Two excellent reviews, both in Volume 6 of "the Annual Review of Plant Physiology," 1955, treat certain aspects of abscission in cotton and other plants (3, 27).

The abscission of the reproductive structures of the cotton plant can occur as floral buds (squares) or as young fruits (bolls) after the flower has opened. Because of shedding, the fruiting potential of the cotton plant seldom is realized. Cotton growers and cotton research workers throughout the cotton-producing areas of the world have been trying to develop methods to prevent shedding. The literature gives the impression that from the late nineteenth century until the present time the favorite cotton research project has been the problem of shedding. Few cotton research workers have resisted the challenge of investigating the mysteries of shedding or the temptation of recording their concept of the cause or causes of this phenomenon.

Until recent years, cotton defoliation has received less attention than shedding. The development of the mechanical harvester, stimulated by serious labor problems arising during and after World War II, emphasized the necessity for understanding the fundamental and practical factors involved in natural and chemically induced defoliation. This impetus has resulted in basic and practical information bearing directly on leaf abscission and other aspects of cotton physiology and production. Results of defoliation research have posed more questions than they have answered and have shown that defoliation is an extremely complicated rather than a relatively simple process.

Many workers have tried to solve the problems of cotton abscission, but we still do not know the basic cause or causes of shedding or defoliation, nor can we always inhibit the former or stimulate the latter as desired in the practical situation. Many theories and combinations of theories have been proposed to explain abscission. Each has been popular during its particular era of postulation and acceptance. All have had inherent weaknesses; the strong point of many is that they have stimulated further research. These theories will be treated in some detail in later sections.

SHEDDING

General

Undoubtedly, many of the early observations on the subject of shedding were never published and many that were are hidden under obscure headings or in publication outlets having limited distribution and no longer accessible to most present day workers. Most of the early workers considered shedding a disease. This concept is reflected by the title of Atkinson's paper, "Some Diseases of Cotton," published in 1892 as a bulletin of the Alabama Station (9). Atkinson, however, apparently considered a disease in its broader definition since he called shedding a "purely physiological trouble" in discussing its occurrence and possible causes. The divergence of opinion in characterizing shedding was still prevalent as late as 1921 when Cook (23) wrote, "Some writers treat shedding as a disease, others consider it a normal habit to reject superfluous buds or young fruits that cannot be matured." Cook also stressed the complexity of shedding and the necessity of treating the problem in its entirety by emphasizing that the primary causes of shedding are genetic and physiological but the method of shedding is morphological.

According to Lloyd (72), the first sound research on shedding in cotton was done in Egypt in 1910 by Balls (10) who recognized both constitutional and environmental causes.

Time, Magnitude and Chronology

Table 1 summarizes representative reports on the magnitude and age of the fruiting forms at shedding for various cottons grown at different locations under different environmental and seasonal conditions. Most of the data are on the shedding of bolls. Apparently, most workers either ignored the shedding of squares or considered it of little consequence. One reason for

this, as pointed out by Eaton (27), is that boll shedding is highly obvious, whereas abortion of squares commonly takes place while the buds are only a few millimeters broad and may not be noted. Ewing (34) reported that natural shedding of floral buds in Mississippi was rarely over 1 to 2 percent and most of this was probably due to bacteria or fungi. Lloyd (72, 73) considered that boll shedding was higher than square shedding in Alabama, but McNamara and Hooten (76) stated that in many seasons in Texas more squares are shed than flowers produced. Hintz and Green (58) also had data showing that three varieties of Upland cotton grown in Oklahoma shed from 62 to 90 percent of the squares formed during the first 10 days of squaring. The Arizona workers (64, 74) show square shedding of 40 to 51 percent. Although Cook (23) has stated that shedding of buds is much less frequent in Egyptian cotton than in Upland cotton, the data of Loomis (74) and Kearney and Peebles (64) show no significant difference in bud shed by Pima and Acala cottons. Harland (54) noted that the extremely high incidence of shedding in Sea Island cotton was due to rains causing extreme floral bud abscission. It appears that square shedding does occur and most workers today recognize its importance. Little work has been recorded on the age of squares when shed. Lloyd (72, 73) reported that buds 36 hours to 10 days old may abscise; after mechanical injury the majority were shed within 5 days but the maximum numbers fell within 2 days. In Arizona, Loomis (74) found that Pima shed its squares at an average age of 15.5 days as compared with 16.5 days for Acala. Compared with bolls, floral buds may abscise at a younger age and be susceptible to shedding for a longer period. In both cases, however, the critical period is the first 10 days.

Most authorities agree that open flowers or flowers at anthesis rarely, if ever, shed. Although Balls (10) reported that shedding takes place entirely at the flower stage, others have interpreted this as meaning after the flowers have opened.

Boll shedding has been more extensively studied than square shedding. Most reports show that 50 percent or more of the flowers produced are shed as young bolls. Boll shedding ranged from 15 to 90 percent. Walhood (83) in a recent review of the subject gave a range of 30 to 70 percent for the average seasonal boll shedding. Hirsutum varieties shed more bolls than Barbadense varieties. The 80 to 90 percent shedding for Sea Island cotton reported by Harland (54) also included flowerbud shedding. The age of boll shedding for Upland varieties usually occurs from 4 to 10 days after anthesis with an average age

TABLE 1. TIME (DAYS) AND MAGNITUDE OF SHEDDING IN COTTON

Worker, location and length of experiment	Species and varieties	Squares		Bolls		Comments
		Age	Percent	Age	Percent	
Ewing, Mississippi, 2 years	G. hirsutum, average of 10 varieties		1-2	7.5-8	60	Shed boll range 4-10 days. Open flowers rarely shed.
Buie, South Carolina,	G. hirsutum				52	Only 15 percent bolls shed during first 3 weeks.
Hintz and Green, Oklahoma	G. hirsutum, 3 varieties		62-90			Shedding for first 10 days of squaring.
McNamara, et al, Texas, 3 years	G. hirsutum, 6 varieties			5.16	66	Many seasons more squares shed than flowers produced.
	Large bolled			4.75	73	
	Small bolled			5.47	59	
Beckett, California	G. cernuum			3.85		
	G. hirsutum			6.10		
Loomis, Arizona 2 years	G. Barbadense (Pima)	15.5	47	10.8	52.0	4-14 days boll-shed period.
	G. hirsutum (Acala)	16.5	51	7.0	86.5	4-10 days boll-shed period.
Kearney-Peebles, Arizona, 2 years	G. Barbadense (Pima)		40.5		15	No significant difference in bud shed.
	G. hirsutum (Acala)		40.0		74	Significant difference in boll shed.
Lloyd, Alabama 2 years	G. hirsutum	5	Lower than bolls	5	60	Range 36 hours-10 days (buds); 4-10 days (bolls); mechanically injured bolls, 2 days; weevil injured, 8 days.
Wadleigh, Arkansas (Greenhouse)	G. hirsutum			4.9-6.1	60-70	Varied N level.
Eaton-Ergle, California and Texas, several years	G. hirsutum				40-65	Higher shed with treatments.
Balls, Egypt, several years	G. Barbadense			4+	40	Constant over years.
Harland, W. Indies, several years	G. Barbadense (Sea Island)		High due to rains		80-90	Highest shedding rates reported.

of approximately 6 days. Large-bolled Hirsutums have a higher shedding percentage and shed at an average younger age than do small-bolled Hirsutums. This also may account for lower shedding in Egyptian varieties. Using Upland varieties, Lloyd (72) reported that mechanically injured bolls usually shed in 2 days compared with an average age of 8 days for boll weevil-injured bolls. Balls (10) in Egypt noted that root pruning and other methods of injury caused consistent boll abscission at about 4 days of age.

From his work in Mississippi, Ewing (34) concluded that there is a normal balance between flowering and shedding regardless of the cause. The cotton plant normally produces many more flowers than it can mature to fruit. Shedding always occurs no matter how favorable the growing conditions for the plant. According to this interpretation the abscission of fruiting forms is a compensating reaction that the plant possesses to prevent overfruiting. The normal relationship of flowering to shedding, when insects and other abnormal factors are controlled, is presented in Figure 1. Although hypothetical, this figure is based on actual data given by Ewing and other workers. Both the flowering and shedding curves approach a sigmoid pattern. At the beginning of the fruiting season, only a small percentage of the forms produced are shed naturally. This has been noted repeatedly by many workers, including Buie (19) in South Carolina, who found that only 15 percent of the flowers produced during the first 3 weeks were shed compared with an overall shedding of 52 percent. In the middle and later weeks of fruiting, the rate of shedding to flowering rises rapidly. For a brief period, shedding exceeds flowering; eventually both processes decline at approximately the same rate as the first fruiting cycle is completed. McNamara and Hooten (76) also emphasized that the largest percentage of the crop is set early; the greatest opportunity for retention of bolls is on the first fruiting branches and the chances of setting bolls on successive fruiting branches are 50 percent less in each instance. In Figure 2, McNamara (76) pictures the production and loss of fruiting forms as a succession of zones—each zone upward and outward from the base of the plant—in which the cotton plant fruits and defruits itself in adjusting crop and growth to available water supply. Although McNamara (76) stressed the zonal fruiting behavior in terms of water availability, Wadleigh (82) has pointed out that it also is applicable to nitrogen supply when water stress was not a factor. It appears that a zonal fruiting behavior pattern would apply equally well to any single factor that alters the fruiting-defruiting balance, providing other necessary factors are not limiting and the growing season is long enough. Such a representation of fruiting behavior has certain limitations in explaining all situations. For example, Eaton (27, 28, 29) emphasized the advantage of removing the early-season flowers and fruits from plants under

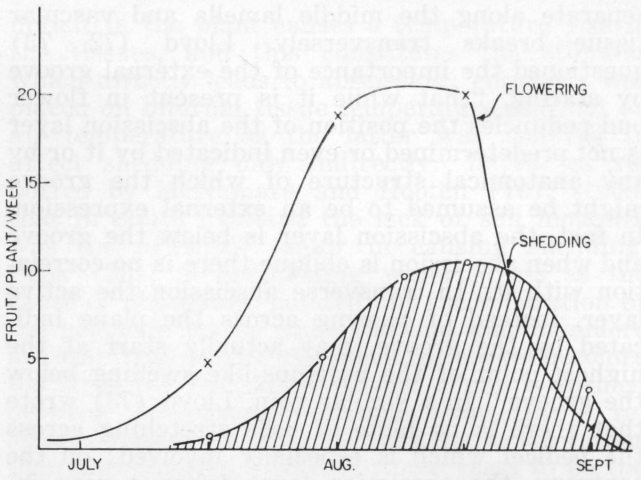


Figure 1. The flowering-shedding cycle in Upland cotton as based on data of Ewing and others.

irrigation as a means of increasing the number of bolls matured. However, under dryland conditions, or where late-season insects are a problem, the advantage of saving the early-fruiting forms becomes of practical importance. Although the goal of the cotton grower is to set both "bottom" and "top" crops, this is seldom realized.

Morphology and Anatomy

Balls (10) in an early paper on shedding reported that anatomically the abscission layer is a simple, single plate of cells, one cell thick, stretching across the stalk in a definite position marked by a faint external groove. Each cell of the plate divides once; the two daughter cells

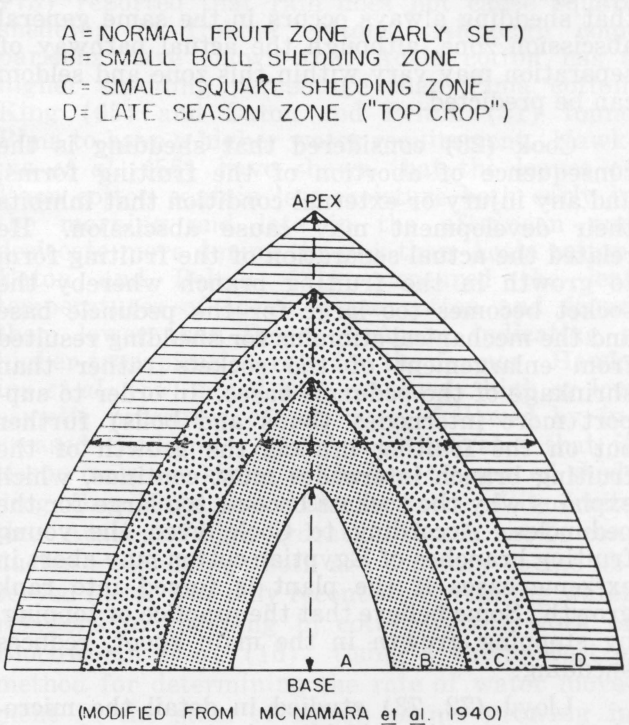


Figure 2. The zonal fruiting-defruiting behavior pattern in cotton.

separate along the middle lamella and vascular tissue breaks transversely. Lloyd (72, 73) questioned the importance of the external groove by stating, "that while it is present in flower bud peduncles the position of the abscission layer is not predetermined or even indicated by it or by any anatomical structure of which the groove might be assumed to be an external expression. In fact, the abscission layer is below the groove and when abscission is oblique there is no correlation with it. In transverse abscission the active layer, instead of passing across the plane indicated by the groove, may actually start at the highest point of the pulvinus-like swelling below the groove." In a similar vein, Lloyd (73) wrote that there is no plate of cells stretching across the pedicel which is especially involved; on the contrary, the abscission layer takes a very inconsistent position and sometimes may even run parallel to the vascular tissue. With decurrent abscission the course of the active layer is still more indeterminate. Briefly, Lloyd (73) believed that the position of the abscission layer is not predetermined by any anatomical relations, but is an expression of a purely physiological phenomenon. Cook (23), replying to Lloyd's statement, pointed out that morphologically the peduncle represents an internode; the points of articulation or sockets on the fruiting branch are nodal parts of unspecialized tissue. Abscission is the result of disarticulation or unjointing of the socket where the base of the peduncle is inserted on the fruiting branch. Therefore, abscission has a very definite morphological position, occurring always at the same place. Lloyd and Cook seemed to be discussing mainly minor details of terminology. Both views can be reconciled by stating that shedding always occurs in the same general abscission zone, although the actual pathway of separation may vary within this zone and seldom can be predicted.

Cook (23) considered that shedding is the consequence of abortion of the fruiting forms, and any injury or external condition that inhibits their development may cause abscission. He related the actual separation of the fruiting form to growth in the fruiting branch whereby the socket becomes too large for the peduncle base and the mechanical stimulus for shedding resulted from enlargement of the sockets rather than shrinkage of the peduncle bases. In order to support more internodes (buds and bolls) further out on the fruiting branch, the growth of the fruiting branch internodes must continue, which explains why the sockets become too large for the peduncles. According to Cook, even the young fruiting branches of Egyptian cotton may abort in extreme cases if the plant is forced into rank growth. Some believe that the practice of topping, by stopping growth in the main shoot, reduces shedding.

Lloyd (72, 73) studied in detail the microchanges attending shedding in cotton and noted that they were essentially the same as in *Mirabilis*. The abscission plane may be confined to a single tier of cells, or may involve two tiers, but rarely more; the older the pedicel, the more indeterminate this will be. Although Lloyd (73) considered abscission a growth process, he stated that whether renewed cell division in the peduncle does or does not occur is of minor importance, but the chemical changes that precede separation and make it possible are of extreme importance. The number of cell divisions observed by Lloyd varied from 0 to 5 and depended to some extent on age of tissues, but more on the rate of abscission, which may be rapid or slow in forms of identical age. Even when cell division occurs, it cannot be stated that it precedes the chemical alteration of the cell walls which allows separation. Lloyd concluded that fruiting form abscission is due to digestion of the middle lamella and adjacent layers of cellulose walls to an extent related to the age of the cells involved and, although division usually occurs, it is not an absolute prerequisite to separation. Lloyd pictured separation proper as being accomplished by chemical alteration of the membranes, preceded by a change in thickness of the existing longitudinal cell walls. Usually thinning of the walls was confined to one region, but some variation was observed. Staining reactions as well as optical qualities displayed by the walls indicated that physical changes are preceded by chemical alterations in the direction of a cellulose mucilage; therefore, the chemical changes are hydrolytic. The actual separation may occur between the last formed membrane and the total remainder of the wall or, if cell division has occurred, the daughter cells may have been loosened from each other. Lloyd (73) noted that in reproductive organ abscission in cotton every phase or method of abscission may be found, from separation of a single layer of cells from another layer to the formation of extensive pockets involving tissues of the stem.

Factors and Theories

General

Eaton (27) pointed out in his recent review that it is more than coincidence that workers in their search for "causes" of shedding have found the latter part of the flowering period, when heavy shedding occurs in waves even under well-controlled conditions in the greenhouse or field, is the most fruitful for investigation. In many cases, the so-called causes proposed under these conditions may, upon thorough examination, actually be secondary or surface factors that induce the more basic underlying reactions leading to the consummation of abscission. Eaton and Ergle (28) have shown that the same "causes" which were associated with late shedding were ineffectual early in the flowering period. The vegetative-reproductive status as well as the fruiting-flowering balance in cotton at the time of studying the "causes" of shedding are impor-

tant. If a plant is already well fruited at the time of heavy late-season flowering, it is inevitable that many of these flowers will be shed first as squares and later as young bolls and the wave of shedding might coincide logically with the imposed or natural environmental conditions under study. Ethylene, which is conducive to heavy shedding, also is stimulatory to further flowering even under adverse environmental conditions (46).

Genetical Causes

Genetic differences in the shedding tendency have been indicated by a number of workers including Balls, Harland, Cook and Kearney and Peebles (10, 23, 54, 64). A thorough genetic study with Pima X Acala crosses by Kearney and Peebles (64) showed that there are genetic factors for shedding which segregate and recombine in the progeny in the expected Mendelian manner. Cook (23) noted that only a genetical basis explains the difference between Egyptian cotton retaining most of the buds and bolls while Upland varieties in adjacent rows are shedding nearly all of their fruiting forms.

Water Relations

Most of the early workers considered that water relations, both too little or too much soil moisture, directly or indirectly caused excessive shedding. Atkinson (9), in 1892, noted that shedding occurred in extremes of wet or dry weather or during rapid change from one to the other extreme. He believed that this was caused by interference with the supply of moisture and nutrient materials to the young forms at the critical period in their development. Balls (10) in Egypt, after several years of observation and experimentation, concluded that a low water content in the plant, whether caused by excessive transpiration or reduced uptake after root pruning, caused shedding. He noted that shedding became abundant toward the end of the irrigation interval and decreased after watering, but became excessive again when the water level was raised by infiltration of flood water from the Nile. Although Atkinson (9) reported that shedding was heaviest in closely spaced cotton, both Balls (10) and Ewing (34) stated that close spacing decreased shedding because it reduced excessive transpiration. The latter interpretation is questionable as the shading effect likely would not compensate for increased foliar evaporating surface or root competition for available moisture with the increase in plant density. In a 2-year study, Ewing (34) noted that shedding was best correlated with low-soil moisture and high-evaporation rates, both affecting plant hydration which had an important bearing on shedding. Lloyd (73) theorized that under field conditions, boll shedding (aside from that due to injury) is attributable to rain or soil-water conditions and that competition between bolls for water causes excessive shedding. He concluded that water deficit in the plant causes a temperature rise in the tissues, and this constitutes the stimulus which directly leads to abscission; emphasis was placed on internal tissue temperature and not on air temperature as the latter was believed to affect shedding only indirectly. Barre, as reported by McNamara and Hooten (76), stated that in South Carolina the lack of soil moisture was the principal factor in causing shedding. Cook (23), in questioning water stress as the cause of abscission, pointed out the separation of the peduncle starts while the bud and involucre are still fresh and turgid, when the socket becomes too large for the peduncle base, a gap is formed between the separating tissues indicating a release of tension. Enlargement of the socket rather than shrinkage of peduncle would seem to be the mechanical stimulus of shedding. In addition to soil-moisture extremes being conducive to shedding, several workers have observed that rain itself favors shedding by pollen destruction and prevention of fertilization; morning rains were more effective than afternoon ones. However, Dunlap (25) reported only slight increases in shedding after wetting open flowers with an atomizer twice daily. He intimated from this and other experiments that cloudy weather associated with rainy periods is more important than the wetting factor. Cook (23) also cited that during cool damp weather, as under high humidity and low temperature conditions in Guatemala, the anthers fail to open, preventing pollination. King (65) noted that heavy rains materially shortened the shedding interval in Pima cotton. Harland (54) stated that Sea Island cotton sheds many of its floral buds during heavy rains, but Lloyd (73) reported that rain does not cause square shedding in Upland cottons. Although comparisons have shown that Acala cotton has a higher shedding percentage than Pima cotton, King (65) and Eaton and Belton (31) found Pima to have a higher water requirement. Hawkins *et al.* (55) have shown that the leaves of Pima cotton contain less moisture both early in the morning and late in the afternoon and desiccate more during the day than Acala cotton. Eaton and Belton (31) measured the leaf temperatures of turgid Pima cotton and found them lower than those of Acala, indicating a higher transpiration rate for the former. Hawkins *et al.* (55) noted that extremely high or low osmotic pressures of sap were followed by increased shedding. All of this indicates that if tissue moisture stress is the basic cause of shedding, then Pima should abscise more of its fruits than Acala and high hydration should not be conducive to shedding; both are contrary to the observed facts. The only recent study relating water relations to shedding in cotton is the work of Bloodworth *et al.* (15). Using a thermoelectric method for determining the rate of water movement in the stem of cotton plants growing in Willacy fine sandy loam and Harlingen clay, these workers observed that squares started

dropping at about 2.5 atmospheres moisture tension in the fine sandy loam and at about 7 atmospheres tension in the heavier clay. The rate of water movement in plants on the above soils dropped to about 30 centimeters per hour when shedding occurred; this represented about 30 percent available moisture in both soils.

Eaton (27) states that the rather common view that drouth causes an unusual proportion of the bolls to shed may originate in part from the fact that late summer drouth often coincides with the period of heavy boll shedding.

Light and Temperature

Most investigators are in agreement that air temperature, with the exception of excessively high temperatures, does not have pronounced direct effects on shedding. However, Cook (23) listed high temperatures as a cause of shedding and Dunlap (25) found high shedding rates associated with temperatures of 100° F. or above both during periods of extended high daily temperature or following briefer periods of exposure to high temperature. Dunlap (24, 25) concluded, however, that the effects of light were more important than either temperature or drouth. Although Lloyd (73) noted that the rate of abscission would change with temperature and related internal temperature to his theory on water deficit as the cause of shedding, he concluded that the effect of air temperature was only indirect. Ewing (34) reported little correlation between shedding and air temperature or relative humidity.

The effects of light upon square and boll abscission also may be mostly indirect. Eaton and Rigler (29), in an experiment repeated under shades in a winter greenhouse and outdoors in the summer, found there was profuse shedding of floral buds under low light intensity. Dunlap (24, 25) noted that periods of cloudy weather during the fruiting period, or treatments involving similar low light intensities for a few days, were followed by increased shedding, and variations in light were more closely associated with shedding than the formation of floral buds. In view of results with other plants, it would appear that excessive high light intensities as well as the spectral quality of radiation would affect shedding; this possible effect on shedding has not been investigated in cotton. Neither have photoperiodic effects on shedding in cotton been reported; apparently it does not directly affect fruiting form abscission in commercial cottons under natural conditions.

Mineral Nutrition, Nitrogen and Carbohydrates

A number of the mineral elements, including N, P, K, S, Mg, Ca, Zn, and B have been reported to affect shedding. In most cases, however, promoting or retarding effects upon shedding have not been consistent nor do they appear to be a direct cause. Ewing (34) compared the percentage shedding of three varieties of cotton grown on a good valley loam soil and a poor hill clay soil. Although the valley plants produced three times more flowers, the average percentage shedding of the three varieties was the same (55 percent) at both sites. Dunlap (25) also found shedding rates remain fairly uniform under conditions of widely varying NPK levels. Eaton (27) pointed out that the uniformity of relative fruitfulness data with varying growths under the influence of varied nitrogen, sulfur and molybdenum supplies, together with the fact that boll shedding is nominal until a good many bolls have been set, suggests more direct causes of shedding. Harland (54), at St. Vincent, concluded that fertilizer level did not have any notable effect upon shedding after finding that checks, P treatment, and complete fertilizer plots averaged 83, 88.5 and 80 percent shedding, respectively. Ewing (34), in Mississippi, in general agreed with Harland's conclusions. In discussing an observation that a 200-pound addition of $NaNO_3$ to cotton in Texas prevented shedding until late in the season, Lloyd (73) thought this was explained in terms of water relations with increased water-holding capacity of the soil due to the fertilizer. Dunlap (25) studying this effect of nitrogen found, in most cases, no marked differences in shedding between high and low N plants as the result of water stress treatments. Using four levels of nitrate supply, Wadleigh (82) reported that regardless of treatment, 60 to 70 percent of all the blossoms produced were shed. The different treatments were accompanied by little variation in the rate of shedding, but N treatment caused marked changes in the absolute number of blossoms shed per plant as well as total number of bolls set. In both sand and water culture experiments, Ergle and Eaton (32) noted that although shedding was slightly higher in high P than low P plants, they concluded that P has no pronounced effect on shedding; the main effect was on fruiting. Ergle (33) had previously reported that cotton plants grown for the first 30 days on complete nutrient solution followed by shifting to a deficient sulfur solution produced about the same number of flowers as those continuously on the complete solution. However, the minus sulfur plants shed 60 percent of their flowers while the high sulfur plants were retaining theirs. Although several workers have alluded to observations that K and Ca deficiencies accelerate shedding, no data are given and direct references cannot be cited. Schappell, Armstrong and Hollis (80) studied the effects of magnesium supply on the shedding of squares and bolls and noted that high magnesium plants shed more squares than plants on low magnesium; boll shedding was approximately the same. This is in direct contrast to the results of a recent and more extensive experiment conducted by Helmy (56) with American Upland and Egyptian Pima cottons showing that magnesium supply had little effect upon square shedding but boll shedding was

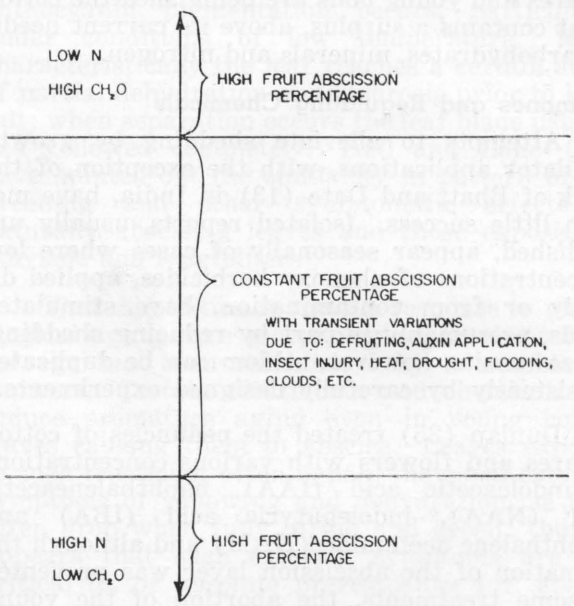
TABLE 2. RELATION OF MAGNESIUM SUPPLY TO FRUITING BEHAVIOR OF EGYPTIAN (PIMA S-1) AND AMERICAN UPLAND (STONEVILLE Z-106) COTTONS AT 85 DAYS OF AGE

Magnesium supply[1]	1/1		1/4		1/16		1/64	
Fruiting behavior	E[2]	U[2]	E	U	E	U	E	U
Average number flowers per plant	19.4	35.6	10.0	27.0	5.9	21.8	2.8	10.8
Percentage shedding	34.6	25.1	44.3	26.8	54.4	54.0	74.0	57.9
Percentage boll set	65.4	74.9	55.7	73.2	45.6	45.0	26.0	42.1
Relative fruitfulness	1.2	3.2	0.5	2.7	0.7	1.9	0.4	1.8

[1]1/1 = Mg. in full-strength Hoagland, other values fractions thereof. All Mg. levels reduced 1/10 at 45 days of age until 85 days of age.
[2]E = Egyptian; U = Upland.

greatly and significantly increased as magnesium supply was decreased. This is shown in Table 2. Of the trace elements, both B and Zn deficiencies have been reported to cause abortions resulting in high shedding. Eaton (30) noted in 1930 that B deficiency caused excessive shedding and believed that it was associated with impaired IAA synthesis and metabolism. In a later review (27) an alternate role, where boron is involved in carbohydrate transport, was suggested. In Zn deficient cultures, Brown and Wilson (17) noted that few floral buds were produced by three species of cotton and those that were produced were shed either as squares or as young bolls.

As pointed out by Eaton (27), beginning with the paper of Mason (75) in 1922, it became popular to believe that the cotton plant retains only as many bolls as it can supply with carbohydrates, nitrogen and other nutrients. This has come to be known as the nutritional theory of boll shedding. In their recent review of 1955, Addicott and Lynch (3) concluded, "To the reviewers the nutritional balance theory adequately explains most of what is known of cotton fruit abscission." Figure 3 from their paper summarizes the common concept relating shedding to the carbohydrate-nitrogen balance and its interrelation with other factors. From cotton plants grown on four serial concentrations of nitrate nitrogen supply, Wadleigh (82) recorded the amount of fruit abscission and the carbohydrate and nitrogen contents. Although he noted little relation between the percentage abscissions and treatment, he did attach significance to the low N and high carbohydrates associated with low nitrogen supply and the reciprocal CHO/N relationship under high N supply as causes of shedding. Although Eaton (27, 29) is credited by some to be one of the early proponents of the nutritional theory, he questions the validity of this interpretation both from his own work and an extensive review of the work of others. In fact, in their most recent paper on the subject, Eaton and Ergle (28) advance rather strong evidence refuting the nutritional interpretation. As shown in Table 3, data from 1947-48 experiments with sucrose, urea, sucrose plus urea, girdling and girdling combined with urea all show a significant increase in shedding over the controls. Although carbohydrate and nitrogen data are given for the various organs, only the middle stem values are given as being representative. The middle stem values, as well as the total plant, in nitrogen or carbohydrate, or their ratios, in the respective treatments are not correlated with shedding in accordance with the CHO/N hypothesis. Other data from their work on seasonal trends in carbohydrate and nitrogen do not support these as the cause of shedding. Carbohydrates increased from mid-July when all bolls were being retained to mid-August when almost all were being shed. Plants from different dates of planting had similar carbohydrate and nitrogen contents in mid-August but vastly different amounts of boll shedding. Also, according to Addicott and Lynch's figure (3), defruiting of plants, as done by Eaton and others which accelerates rapid carbohydrate accumulation and a corresponding decrease in nitrogen, should cause excessive shedding of subsequent set fruiting forms. This was not the case as higher yields were obtained than from untreated normally fruiting controls.



RELATION OF FACTORS KNOWN TO AFFECT FRUIT ABSCISSION IN COTTON (AFTER ADDICOTT 1955)

Figure 3. The nutritional (carbohydrate-nitrogen) theory of shedding in cotton.

TABLE 3. EFFECT OF SUCROSE AND UREA SPRAYS AND GIRDLING UPON PERCENTAGE SHEDDING AND CARBOHYDRATE AND NITROGEN COMPOSITION AS PERCENTAGE FRESH WEIGHT[1]

Treatment	Percent shedding	Sugars + starch		Total N	
		Middle stems	13-day-old bolls	Middle stems	13-day-old bolls
1947, July 3-August 21	Average of 6 plants sprayed 6 days a week[2]				
Water controls	57	1.34	2.16	0.22	0.30
20 percent sucrose	70	1.04	2.08	0.21	0.29
1 percent N (urea)	66	0.93	1.97	0.25	0.36
Sucrose and N	88	1.16	2.21	0.23	0.33
1948, August 4-29	Average of 10 plants sprayed on alternate days[3]				
Controls	62	1.17		0.17	
2 percent N (urea)	78	0.80		0.22	
Girdle	87	2.51		0.16	
Urea and girdle	92	1.97		0.25	

[1]Data from Eaton and Ergle, 1953.
[2]Mean of collections July 16 and 31 and August 14.
[3]Sampled 1 week after treatment.

From the data discussed above and other not cited, it appears that although carbohydrates and nitrogen affect shedding, either singly or in combination, the CHO/N ratio *per se* is no more likely to be the basic cause of shedding than it is the basic cause of flower inception, as once so widely postulated. Any attempt to explain shedding in terms of nutrition alone must also reconcile the fact that usually at the time that squares and young bolls are being shed the cotton plant contains a surplus, above its current needs, of carbohydrates, minerals and nitrogen.

Hormones and Regulating Chemicals

Attempts to alleviate shedding by growth regulator applications, with the exception of the work of Bhatt and Date (13) in India, have met with little success. Isolated reports, usually unpublished, appear seasonally of cases where low concentrations of phenoxy herbicides, applied directly or from contamination, have stimulated yields, presumably in part by reducing shedding. These results, however, seldom can be duplicated consistently by carefully designed experiments.

Dunlap (25) treated the peduncles of cotton squares and flowers with various concentrations of indoleacetic acid (IAA), naphthaleneacetic acid (NAA), indolebutyric acid (IBA) and Naphthalene acetamide (NAM) and although the formation of the abscission layer was prevented in some treatments, the abortion of the young bolls was not prevented. Dunlap noted increased shedding with increased hormone concentration and concluded that in general there were no significant effects in preventing abscission.

From experiments with dust and spray applications of NAA, chlorophenoxyacetic acid (CPA) and β naphthoxyacetic acid (NOA) at Shafter, California, and College Station, Texas, when high boll shedding was occurring, Eaton (26) reported no effect on boll retention; 20 p.p.m. of CPA reduced the number of bolls significantly. Neither did sprays alter the proportion of fruiting to vegetative branches in short day or day neutral cottons.

Bhatt and Date (13), using an improved strain of Bhoj (*G. arboreium*), applied NAA as a spray at 10, 20 and 30 p.p.m. at the active vegetative stage and at the onset of reproduction. The early spray at 10 p.p.m. and all late sprays caused a statistically significant increase in seed cotton. Repetition of this experiment in unpublished work by Hall (39) using both NAA and NAM on Deltapine cotton gave yields that were not significantly different from the unsprayed controls; shedding rates were approximately the same. In an unconfirmed experiment Johnson and Cowley (61) noted that plants from seeds impregnated with low concentrations of growth regulators set bolls at lower nodes and had less early-season shedding than controls.

Eaton (27, 28) has also reviewed other work on growth regulators and concluded that independent of major effects upon growth, such materials have been without pronounced effects upon fruiting behavior.

Carns *et al.* (20) reported that they were unable to detect measurable auxin by the *Avena* curvature test from young bolls when placed upon agar blocks, but when similar bolls were placed on blocks containing 100 micrograms of IAA, the IAA activity rapidly disappeared. After ether extraction of carpellary boll tissue and chromatographic separation and identification, Hacskaylo and Carns (38) reported four areas of activity: at Rf 0.95, acceleration characteristic of ethyl ester of indoleacetic acid; at Rf 0.90, inhibition; at Rf 0.88, acceleration; and at Rf 0.68, acceleration characteristic of indoleacetic acid. Activity was measured by the *Avena* curvature test. Further studies by Carns *et al.* (20) on the chromatographic separation of the growth retarding and growth-promoting substances from carpellary extracts of 4-day-old bolls gave a net overall growth-retarding effect equivalent to the inactivation of 19.4 micrograms per liter of IAA. Carns *et al.* termed this substance an inhibitor and studied its relationship to boll abscission. They found that inhibitor activity within the diffusate increased with boll age, reaching a maximum just prior to the time when bolls normally abscise, but decreased rapidly thereafter. Diffusate activity and the quantity of extractable inhibitor from carpellary tissue were not the same and varied between varieties.

Field observations in Texas, during 1955-57 within a 2-mile radius upwind from an industrial

plant discharging considerable ethylene into the atmosphere, showed excessive bud and boll shedding, breaking of apical dominance and forcing of lateral buds, and greatly stimulated flowering (46). It was not uncommon to count several hundred squares per plant in fields closest to the ethylene source, yet these were shed as squares or young bolls to the extent that total loss of yield resulted. In basic studies Hall *et al.* (46) found that the first significant increase in ethylene production by untreated cotton was associated with the onset of the reproductive stage.

Eaton (27) has suggested that boll shedding is controlled by a balance between auxin produced in the leaves and an anti-auxin or inhabiting material produced in developing bolls. These interact in the fruiting branches and regulate the abscission of young fruit. Wadleigh (82) had previously postulated that when biochemical equilibria are shifted in the direction causing a limitation on supplies of one or more essential constituents to developing bolls, a stimulus is set forth, which induces the formation of the abscission layers of the peduncle of excess bolls and squares. He suggested that gametic union becames the impetus for the formation of a hormone which is stimulatory to the formation of the abscission layers on other reproductive organs. Addicott and Lynch (3) state that the requirements for Wadleigh's theoretical hormone are completely met by auxin which is produced by many developing fruits. They believe that since young fruits produce less auxin than older fruits and since nutrients often are mobilized to sites high in auxin, this causes young fruits to receive fewer nutrients, leading to impairment of auxin production and resultant abscission. However, other facts, such as the increasing ability of tissue to inactivate auxin with age, the general lack of added auxin to prevent shedding, and in some cases the abscission of squares and young bolls while still high in nutrients, would have to be reconciled in terms of the above interpretation before it can be accepted without reservation.

With the addition of the "cinderella" group, the gibberellins, to the ever-growing family of regulating chemicals, another approach to the problem of shedding was opened up to research workers. Walhood (84) has reported that controlled application of gibberellic acid to cotton forms will drastically alter shedding and that apparently there is a compensating interaction with auxin. However, other workers, notably Johnson (62) and Arndt (8), have reported that whole plant spraying of gibberellic acid under field conditions is far from being at present the practical solution to shedding. This is not meant to denote that the gibberellins are not involved in the fruiting-shedding mechanism. The existence of gibberellin-like compounds in green plants and their possible role in many functions is sufficient basis alone for intensified basic research as to their possible role in the fruiting-shedding balance mechanism in cotton.

The discovery of an abscission-promoting but growth-inhibiting factor in mature cotton leaves by Herrero and Hall (57) and its apparent similarity to the inhibitor from young bolls (20) merits accelerated research along these lines.

Conclusions

Eaton's (27) statement that it is necessary to conclude that the basic cause or causes of boll shedding are unknown, is inevitable in light of present evidence. Undoubtedly the most fruitful avenue of future investigation in finding the basic cause of shedding appears to be in the growth-regulating balance reactions of the cotton plant. Understanding of the specific enzyme systems involved and how these interact with promoting and inhibiting regulating factors should be the ultimate answer to the basic cause of abscission. When all facts are reviewed, one must conclude that the fruit itself and the vegetative status of the plant at the time of reproduction are key factors in determining whether young fruiting forms will be retained or shed.

LEAF ABSCISSION

General

Natural defoliation usually is initiated in the mature basal leaves after a certain stage of senescence or aging is attained. Certain preabscission changes have been observed to precede the actual separation process. Occasionally anthocyanin pigmentation occurs, particularly under conditions of low temperature. More characteristically the leaf reaches a certain stage of partial dehydration and chlorosis prior to leaffall; when separation occurs the leaf blade usually has yellowed completely. Hall and Lane (42) have pointed out the similarity in pattern of degreening and other symptomatic effects in naturally abscising leaves and those exposed to ethylene and a defoliant.

That defoliation is more a response to physiological aging than morphological or chronological age has been established by a number of workers. Certain treatments and chemicals can induce premature aging even in young cotton leaves causing them to abscise. Leaves exposed to such treatment often bypass the usual external symptoms of yellowing and dehydration, as they often drop when fully turgid and green; thus, it appears that such external symptoms are not critical to, or absolute prerequisites for, abscission.

Induced defoliation usually is preceded by some degree of injury to the blade or petiole. Mechanical or physical, chemical and biological

injury all initiate and accelerate leaf-fall. Hall (40), Hall and Lane (42) have shown that complete deblading enhances abscission while Jackson (59) found that the rate of defoliation was proportional to the amount of the leaf blade removed. Chemical injury by defoliants apparently has a similar effect. Jackson (59) treated different portions of the upper surface of mature cotton leaves with monosodium cyanamide and obtained the greatest response by treating the entire surface and progressively less response when three-fourths, one-half and one-fourth of the leaf surface was treated; a greater response resulted by treating the basal half of the leaf compared with treating the upper or lateral halves. Addicott and Walhood (7) noted that a chlorate-borate defoliant applied to both blade and petiole shortened the time of abscission compared with application only to the blade; the rate of abscission was extremely slow when the defoliant was applied only to the petiole. Lane and Hall (42) and Hall (48), however, found that the highest percentage abscission was obtained in fewer days by treating debladed petiole ends with Endothal, but that Endothal differed from the chlorate-borate defoliant used by Addicott and Walhood (7) both in the rate and final percentage abscission obtained in 18 days. Commercial and experimental defoliants cause widely different types of injury as reported by Johnson (60). Chemicals that cause mild injury are usually the most effective defoliants while extremely caustic, toxic and desiccating types result in rapid tissue inactivation, death and "freezing" of the foliage. Hall *et al.* (43, 44) and Eaton (27) concluded that there is little correlation between chemical structure of defoliating chemicals and physiological activity, but many tend to be oxidizing agents and all have a common injurious effect which initiates the changes culminating in abscission. Addicott *et al.* (4) arrived at a similar conclusion after studying six compounds and noted that over a wide range of concentrations the compounds did not accelerate the rate of abscission when applied directly to cotyledonary node explants. Based on their results they stated that the function of defoliants is to initiate, rather than accelerate, abscission.

The exact number of chemicals screened for abscission agents by private, public and commercial workers using cotton and other test plants is unknown. Of the probable thousands screened, the majority have had relatively low or no activity.

Biological injury from insects and microorganisms causes leaf-fall. Rather severe defoliation occurs in fields heavily infested with bacterial leaf spot; verticillium and fusarium wilts of cotton cause some defoliation.

It can be noted that injury is not always manifested macroscopically and may be physiological or biochemical. From this viewpoint, even natural defoliation that results from mineral deficiencies and senescence actually may be the result of a "physiological injury mechanism." Further example of such an effect is exemplified by the result of low temperature on cotton grown on the High Plains of Texas. If the first fall frosts are light, the leaf blades are injured without any marked external symptoms of damage but abscission is initiated and defoliation results. On the other hand, a heavy frost or sudden freeze browns or marks the foliage and usually kills the abscission zone and stem; the leaves progressively dry and though some may be removed by the wind, the bulk remain attached until removed by the mechanical stripper.

Addicott and Lynch (3) called attention to the striking similarities between the factors that control the growth of lateral buds and abscission. This is particularly applicable to cotton defoliation. Deblading or injury to the blade by defoliants stimulates abscission and the growth of axillary buds. Under conditions of adequate soil moisture the rapid and profuse regrowth defeats the practical purpose of defoliation. Most commercial defoliants have little inhibiting effect upon regrowth and even stimulate its development. The discovery by workers of the Texas Station (44) that amino triazole possessed both defoliating and growth-inhibiting properties has been a step in the direction of a practical solution to the problem. It also indicates that the suggestion by several workers that leaf abscission is basically a growth process is untenable.

Morphology and Anatomy

Gawadi and Avery (37) studying leaf abscission in selected plants placed cotton in Type 1, those species that naturally exhibit secondary cell division at the base of the petiole, thus forming the traditional abscission layer prior to abscission. They used immature leaves and by deblading and applying several defoliating agents followed abscission anatomically. In naturally abscising cotton leaves the histological changes were much the same as in poinsettia; the abscission layer usually did not exceed two to three tiers of cells dividing in more than one plane but usually diagonally. When abscission was induced in young leaves by deblading, cell division was induced in the abscission zone and the petioles fell in 4 to 5 days. Ethylene chlorohydrin caused abscission in 1 to 3 days without cell division in young leaves. Petiole stumps treated with a 1 percent lanolin paste of B-naphthoxyacetic acid abscised as readily as untreated debladed checks but the compound inhibited the formation of the abscission layer (no secondary cell division). From this work Gawadi and Avery (37) concluded that the abscission layer is not necessary for abscission. Lane (66) studied the histological changes in healthy fully expanded cotton leaves at several stages following the application of Endothal to the blades. Cell division was observed in the abscission layer, but separation followed a

very irregular course through the abscission zone with hydrolytic phenomena playing a dominant part in the later stages of the process. A more comprehensive investigation of the macro and microscopic changes associated with natural and defoliant induced abscission in four age classes of leaves was conducted by Leinweber and Hall (69, 71). The age classes were as follows: Class I, immature blades without a well-defined pulvinoid region, no abscission zone as such and no cell differentiation. Class II, mature blades and beginning of pulvinoid region but no cell differentiation in abscission zone. Class III, mature blades and well-developed pulvinoid region but no cell differentiation in abscission zone. Class IV, mature blade, well-developed pulvinoid region and cell differentiation or abscission layer present in abscission zone. These have been illustrated (69).

It was found that macroscopic changes indicative of the ultimate pattern of abscission occur rather early in the ontogeny of the mature leaf. Initially a slight depression, groove or recessed collar often circumferentially delimits the abscission zone at the base of the petiole. With progression of leaf maturation a narrow, slightly yellow to hyaline area is discernible in the abscission zone; soon after, parting of the epidermis on the abaxial side of the petiole is initiated. Separation of the petiole from the stem proceeds in an angular direction toward the adaxial surface with usually a small group of cells on the upper surface of the petiole being the last connective tissue to resist complete separation. Some exceptions to this usual pattern of separation have been noted. Essentially the same pattern and sequence of events described for natural abscission are followed very closely, but at a much accelerated rate, when defoliants are applied (69, 71).

The initial stage in natural leaf abscission detected microscopically is a partial dissolution of mature cell walls in the abscission zone. This event is closely associated with the formation of the hyaline region that can be observed macroscopically. Following closely cell wall modification, there is usually a layer of cells in the modified zone that begins to divide on the abaxial side. A tier of very small cells forms rapidly but along an irregular course across the petiole toward the adaxial side. This layer, in agreement with Gawadi and Avery's observation, is two to three cells wide, and frequently separation of the petiole along this zone of weakness progresses almost as fast as the layer is formed. Separation of vascular tissue appears to be partly mechanical, however, there is evidence also to indicate at least partial dissolution of the vascular tissues with phloem cells dividing much the same as the collenchyma cells. Little or no cell-wall formation occurs between the newly divided cells and in most cases dissolution of the middle lamella occurs. Both contribute to a greatly weakened condition of the petiole in this zone. Frequently binucleate cells are formed, possibly due to failure of the cell plate to form. Separation of the petiole follows the weakened abscission zone very closely even across vascular tissues. Seven to 10 days following, leaf-fall phellogen and phelloderm layers are readily perceptible across the abscission wound and appear to arise from continuation of the cork cambium of the main stem. Chemically induced leaf abscission by use of disodium 3, 6-endoxohexahydrophthalate (Endothal), sodium chlorate-borate (Shed-A-Leaf), 3-amino-1,2,4-triazole (ATA) and ethylene follows diverse patterns. Endothal induces much the same response sequence as observed in natural abscission. On the other hand, Shed-A-Leaf, amino triazole and ethylene stimulate little cell division. Their chief influence on the abscssion process appears primarily to be promoting dissolution of cell walls in the abscission zone. It appears that the main factor governing whether cell division takes place is the rate of abscission. In cotton, cell division appears to be a secondary side reaction of abscission and not the stimulus to, or the primary cause of, separation. Figure 4 illustrates some of these macro and microscopic changes. Indoleacetic acid and naphthaleneacetic acid applied proximally to the abscission zone inhibited the formation of the abscission layer and although retarding did not entirely prevent abscission. The results of Leinweber and Hall (71) accord well with those of Gawadi and Avery (37). The series of morphological and anatomical changes previously described by Lloyd (72, 73) for fruiting form abscission in cotton and those described for foliar abscission are strikingly similar.

Physiology

Water Relations

Although the effects of soil moisture on defoliation are mostly indirect, the water relations during the growth cycle of the cotton plant appear to be one of the critical factors regulating good field defoliation and causing variability in results with the same defoliant. A sudden deficiency of water usually causes the cotton plant to drop its lower leaves; whereas when drouth develops slowly and becomes pronounced towards the end of the growing season, leaf abscission is retarded and chemical defoliation becomes extremely difficult. These conditions frequently are encountered in the High Plains of Texas and Oklahoma and occasionally in other areas. Research (2) suggests that defoliants do not penetrate readily into leaves of moisture-stressed plants; this in part may explain the poor defoliation usually obtained under such conditions. Vernon Hall (52) noted that plants grown under water stress at two levels of soil fertility and three levels of boll load consistently gave poorer defoliation with two types of defoliants than plants receiving adequate moisture. He believed

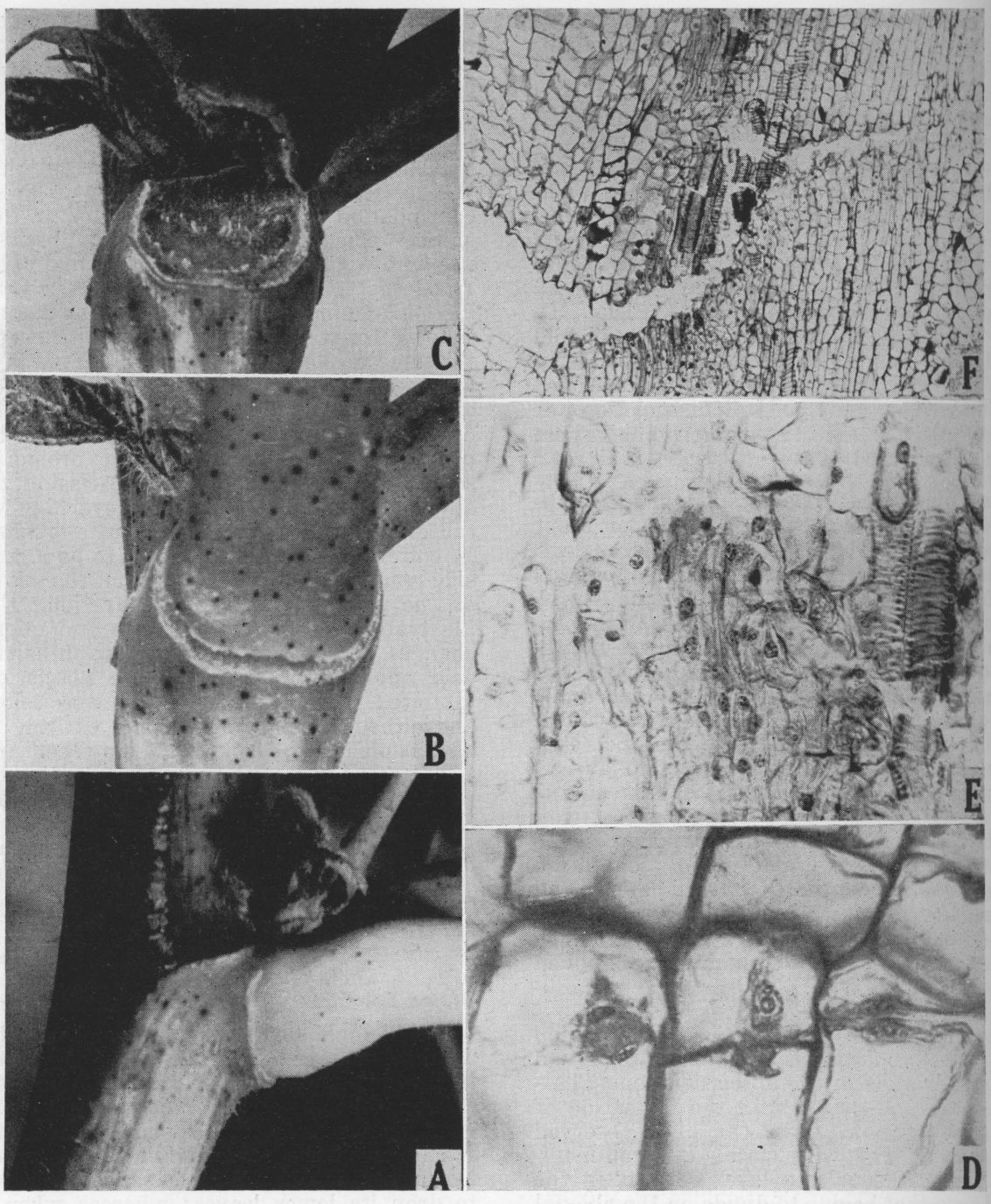


Figure 4. Visual and microscopic changes occurring during cotton defoliation: A, B, and C—progressive visual changes in abscission of cotton leaves. D, E and F—progressive microscopic changes in cotton-leaf abscission zone leading to separation; magnification 780, 210 and 50 times, respectively.

that the difference was due to the effect upon the starch content of the foliage. Thaxton *et al.* (81) have shown that late irrigations at Lubbock, Texas, lower chemical defoliation an average of 20 percent; this has also been observed in the Lower Rio Grange Valley of Texas. Reviewing cotton production practices affecting defoliation, Harrison (53) stated that a constant soil-moisture level, high enough to maintain a uniform rate of growth throughout the growing and fruiting life of the crop, contributes much to the success of defoliation at maturity. Harrison pointed out that cotton growing on poorly leveled land with high and low spots, or on fields with alkali spots or sandy strips causing poor moisture retention and avaliability, defoliates poorly.

Texas Agricultural Experiment Station workers have reported results bearing on moisture and defoliability. A comparison of six defoliants applied to dryland and irrigated cotton in the Lower Rio Grande Valley showed that four of the six compounds gave better defoliation on

irrigated cotton (50, 51). At Temple, Texas, soil moisture samples on three soil classes were taken throughout the growing season (22). In general, soil moisture declined with the advance of the summer and most defoliants were more effective at the higher moisture levels; the soil class having the lowest available moisture at the time of defoliation gave the poorest results. At College Station a 2-year supplemental irrigation study showed that the plots receiving no irrigation gave the lowest defoliation, the medium moisture levels gave the highest, followed by slightly lower defoliation at the high moisture levels (50, 51). With the larger, leafier plants on the high moisture levels, coverage was a factor in explaining poorer defoliation due to inadequate penetration of the defoliant. Using a thermoelectric method for following the rate of water movement in the stems of cotton plants treated with a defoliant, Bloodworth *et al.* (15) noted a gradual decrease in the rate of water movement following application of a mild injury-inducing defoliant until defoliation occurred, followed by an increase with the appearance of secondary growth (Figure 5). A desiccant caused a sharp initial decrease until the appearance of regrowth. Hall and Lane (42) and Johnson and Hall (63) found a decrease in leaf hydration following the application of chemicals; the more toxic the defoliant the higher the rate and amount of desiccation. Brown and Addicott (16) considered that water relations are important in abscission and a rapid change in water relations often precedes leaf-fall in the field. They suggested that turgor regulates the tissue tensions and compressions within the abscission zone and facilitates mechanical separation. Hall (40) concluded that water relations were not the basic cause of abscission but functioned only indirectly by possibly reducing auxin content, increasing ethylene production or by facilitating mechanical separation. In the case of dust defoliants, such as calcium cyanamid, high relative humidity or leaf moisture (surface or transpirational) are necessary to activate the compound.

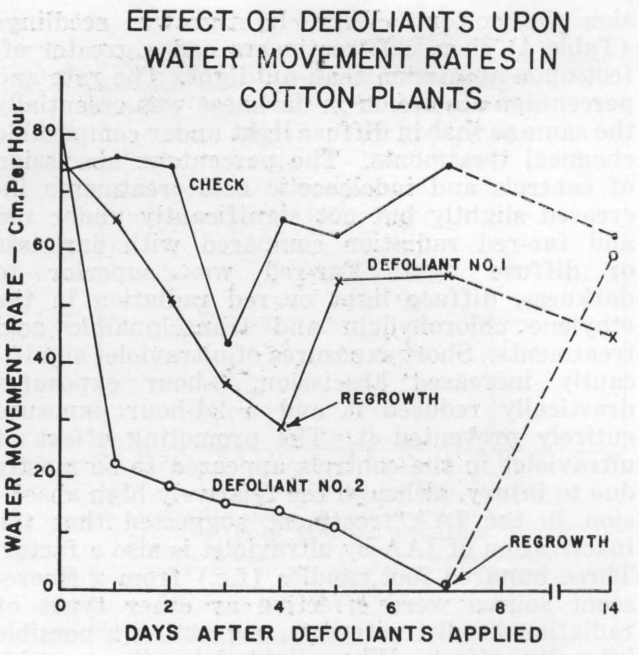


Figure 5. Effect of two defoliants upon water movement rates following application. (After Bloodworth et al., 1956.)

Light and Temperature

Field observations have indicated that the best chemical defoliation of cotton usually occurs under bright conditions of high light intensity. Lane and Hall (67) reported that chemical defoliation of intact mature cotton plants was more effective at light intensities above 3,000-foot candles and that defoliation was poor in starch-depleted plants or in the dark unless sugar was supplied. It was believed that the effect of light was primarily upon the absorption and translocation of the defoliant and that high light intensity is associated with acceleration of chemical injury and leaf dehydration as both appear to be an integral part of successful field defoliation. A recent study by Hall and Liverman (45) investigated the qualitative and quantitative aspects of radiation and chemicals upon cotyledon abscis-

TABLE 4. EFFECTS OF LIGHT AND GROWTH REGULATORS ON THE AVERAGE PERCENTAGE ABSCISSION IN 12 DAYS AND THE DAYS TO 50 PERCENT ABSCISSION IN COTTON[1]

Light treatment	Lanolin control		1 percent IAA		1 percent ECH		1 percent TCA	
	Percent in 12 days	Days to 50 percent	Percent in 12 days	Days to 50 percent	Percent in 12 days	Days to 50 percent	Percent in 12 days	Days to 50 percent
Dark control	5	18	3	18	63	2.0	89	2.0
Room light	4	18	0	18	69	2.0	84	2.5
Red	17	16	17	18	86	2.5	80	2.5
Far-red	13	16	11	18	94	1.5	96	1.5
Fluorescent	35	16	18	18	90	1.5	100	1.5
U.V., 1.5 hours	38	14	57	2	100	2.0	96	2.0

Values required for significance for:

	Percent abscission in 12 days		Days to 50 percent abscission	
	Light[2]	Chemicals[2]	Light[2]	Chemicals[2]
.01 level	2.64	2.16	0.70	0.59
.05 level	1.69	1.62	0.53	0.45

[1]Each datum represents the mean of 96 petioles.
[2]Light x chemicals interaction is highly significant.

sion in cotton. With light-grown seedlings (Table 4) chemical treatments had a greater effect upon abscission than did light. The rate and percentage abscission in darkness was essentially the same as that in diffuse light under comparable chemical treatments. The percentage abscission of controls and indoleacetic acid treatments increased slightly but not significantly under red and far-red radiation compared with darkness or diffuse light. Far-red was superior to darkness, diffuse light or red radiation in the ethylene chlorohydrin and transcinnamic acid treatments. Short exposures of ultraviolet significantly increased abscission, 3-hour exposures drastically reduced it and a 24-hour exposure entirely prevented it. The promoting effect of ultraviolet in the controls appeared to be mostly due to injury, although the relatively high abscission in the IAA treatment suggested that the inactivation of IAA by ultraviolet is also a factor. Three hundred foot candles (f.c.) from a fluorescent source were effective as other types of radiation in all treatments, suggesting a possible intensity effect. When light intensity was investigated (Figure 6) abscission in the controls was promoted by increasing intensities up to 2500 f.c. Although abscission in the IAA treatment was reduced compared with the control, it paralleled rather closely the light intensity curve of the control. Increasing light intensity had less effect on abscission in the ECH treatment. Light intensities of 6,000 to 8,000 f.c. significantly reduced abscission in all treatments. The effects of

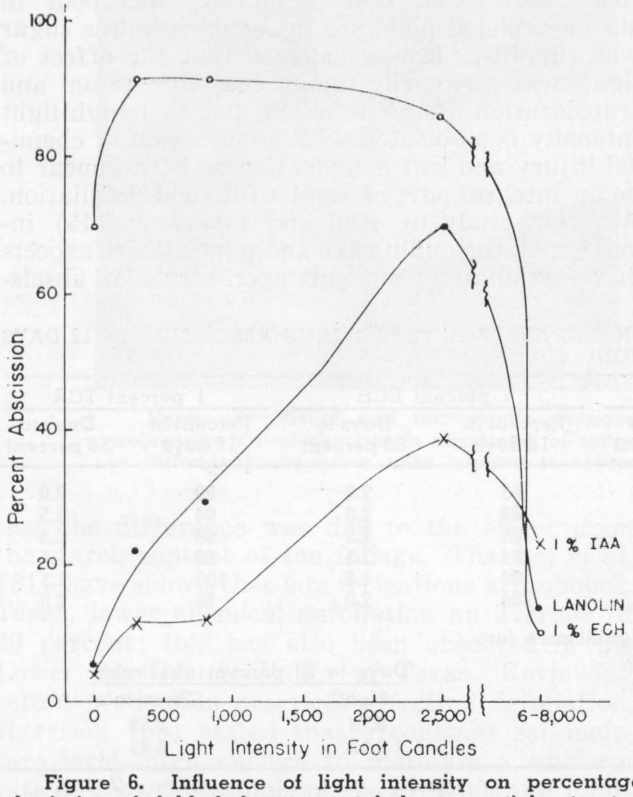


Figure 6. Influence of light intensity on percentage abscission of debladed cotton cotyledonary petioles treated as indicated. (After Hall and Liverman, 1956.)

high light intensity on debladed petioles may be indirect through rapid tissue dehydration and inactivation. Brown and Hyer (18) studied the effects of various lengths of darkness prior to, during and after, and after the application of defoliants and IAA on defoliation in three varieties of cotton and compared these treatments to comparable plants under normal light-dark regimes. It was noted that the "darkness" treatments reduced defoliation significantly compared to controls; the longer periods of darkness gave the greatest reduction in defoliation. Indoleacetic acid gave a significant reduction in defoliation and the reduction was similar, regardless of darkness or control treatments. The three varieties reacted similarly to chemical and dark treatments.

The effects of photoperiod upon defoliation have not been investigated in cotton; results with other plants suggest that any possible effects would be indirect.

With cotton, it is doubted that temperature has any direct effect in inducing natural or chemically initiated defoliation, although increasing temperature up to 35° C. accelerates the velocity of abscission as would be expected for biological reactions. Lane and Hall (67) obtained less defoliation at lower temperatures than at higher temperatures under different light intensities. Abscission was studied in untreated and Endothal-treated intact and debladed main stalk leaves at temperatures from 5 to 35° C. in 5-degree intervals by Lane *et al.* (68). No abscission had occurred at 5° C. by 21 days in any treatment, whereas at 10 and 15° C. only from 25 to 40 percent of the defoliant-treated blades and petioles had abscised. Between 15 and 35° C., the rate of chemically induced abscission increased twofold or more with each 10° C. change. From 20 to 35° C., treated blades abscised more slowly than debladed treated petioles; at temperatures below 20° C., this lag was more pronounced and the percent abscission was more variable between replicates and greatly reduced compared with higher temperatures. The rate of natural abscission in untreated petioles was considerably slower and less consistent than that induced by Endothal. The effect of temperature upon the rate of natural or chemically induced abscission was, however, in general agreement. It has been observed that field defoliation is reduced by temporary low temperature conditions in the summer and is especially retarded by declining night temperatures in the fall.

Mineral Nutrition, Nitrogen and Carbohydrates

Deficiencies of almost all of the mineral elements have been reported to cause some degree of premature leaf abscission; those that cause high leaf-fall are calcium, magnesium, potassium and zinc. The effects of calcium and magnesium may be due to their role in pectate salt formation in the cell walls; whereas zinc is required for

auxin synthesis. Sulfur (33), magnesium (56) and zinc deficiencies (17) cause both shedding and defoliation, probably through the same mechanism. Harrison (53) considered that the level of soil fertility, particularly nitrogen, was an important factor in chemical defoliation. Under California conditions, Harrison believed that the best defoliation was obtained when the entire nitrogen fertilizer supply was applied early in the season so that it was low or exhausted at the time of defoliation. However, in Texas it has been observed that plants showing pronounced nitrogen deficiency at harvest defoliate poorly with chemical defoliants. An ammonium nitrate fertilizer test, applied in 1951 at Lubbock, Texas, before planting, had little effect on the response to defoliation; anhydrous ammonia applied in several ways and at different dates inhibited defoliation (81). The available nitrogen status in three plots was studied throughout the growing season at Temple, Texas (22). Little correlation existed between nitrogen and the defoliation obtained in the three plots under the season's conditions. The effects of NPK fertilization, singly and in combination, were studied at three locations in Texas during 1953 (50). The fertilizers, alone or in combination, had no significant effect on defoliation at the three locations, but defoliation differed from one location to another. Under conditions where moisture is limiting, an effect of fertilizers upon defoliation would not be expected.

Vernon Hall (52) controlled the carbohydrate and nitrogen contents of the foliage by varying fertility, moisture and boll load and found an inverse correlation between starch levels and the effectiveness of two defoliants. He stated that although there appeared to be a significant positive correlation between the percent defoliation and total nitrogen content of the leaves, this effect was due to intercovariance between starch and total nitrogen. He concluded that the susceptibility of a cotton field to chemical defoliation could be predicted by making a starch assay of the plants. Hall and Lane (42) however, found, both in tests with potted plants and at four Texas field stations, little evidence for any correlation or definite trends between the carbohydrate and nitrogen fractions of the leaves and the percentage defoliation obtained in 1950-51. Rather the correlation appeared to be an interaction between defoliant treatment and leaf composition during the defoliation process more than between the original carbohydrate or nitrogen levels. These changes are illustrated in Figure 7. In a later paper, Hall *et al.* (44) reported that amino triazole-treated cotton plants showed compositional changes following application. The aerial organs lost approximately half of the original reducing sugars and sucrose; a slight increase in starch was essentially balanced by an equivalent loss in the hemicellulose fraction. The net result was a decrease in the total carbohydrates. Preliminary experiments showed changes in nitrogen, potassium and phosphorus in amino triazole-treated plants, but calcium values were relatively unaffected. Leinweber and Hall (70) have studied the effect of defoliants upon the initial chemical changes in the cotton leaf blade. The results indicated that compositional changes occur with aging and the initiation of foliar abscission. During the initial stages of leaf abscission, changes in nitrogen fractions appeared more critical than carbohydrate alterations; significant changes in the inorganic components of the blades did not occur during the first 10 hours following defoliant application (70).

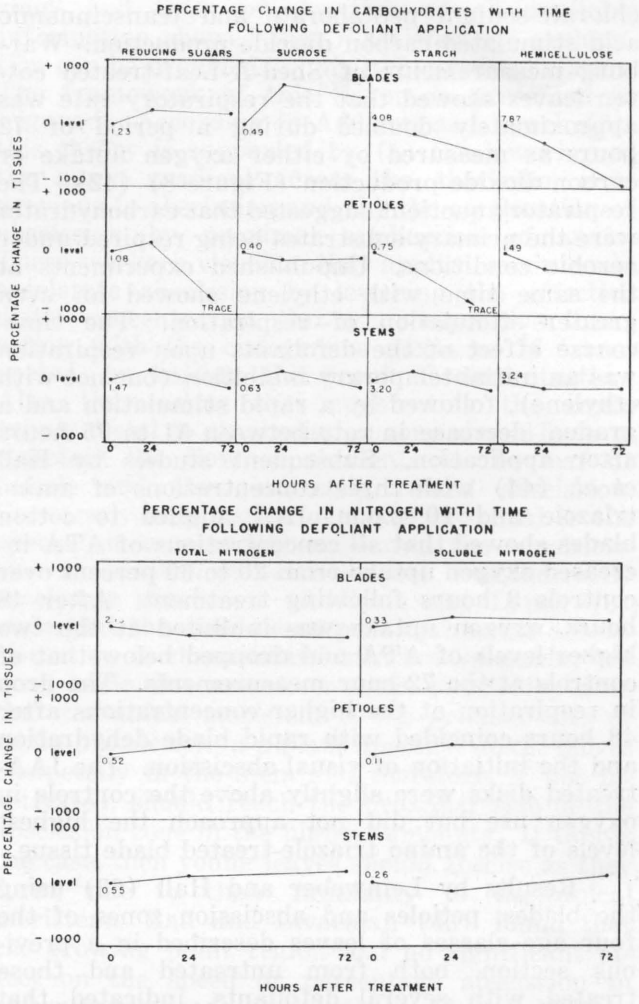


Figure 7. Changes in nitrogen and carbohydrate fractions as percentage dry weight during defoliation. (After Hall and Lane, 1952.)

Respiration

Respiration is implicated in abscission; according to Addicott and Lynch (3) the complete process may be essential. Dead leaves, particularly those that are killed rapidly, do not abscise, and cotton plants with low metabolic activity defoliate slowly, if at all.

In experiments with mature cotton leaves, Hall (41) demonstrated that Endothal, sodium

chlorate-sodium pentaborate and transcinnamic acid stimulated carbon dioxide production. Warburg measurements of Shed-A-Leaf-treated cotton leaves showed that the respiratory rate was approximately doubled during a period of 72 hours as measured by either oxygen uptake or carbon dioxide production (Figure 8) (42). The respiratory quotient suggested that carbohydrates were the primary substrates being respired under aerobic conditions. Unpublished experiments at the same time with ethylene showed an even greater stimulation of respiration. The time-course effect of the defoliants upon respiration was an initial temporary inhibition (but not with ethylene), followed by a rapid stimulation and a gradual decrease in rate between 51 to 75 hours after application. Subsequent studies by Hall *et al.* (44) with three concentrations of amino triazole and 10 p.p.m. IAA applied to cotton blades showed that all concentrations of ATA increased oxygen uptake from 20 to 60 percent over controls 3 hours following treatment. After 48 hours, oxygen uptake was inhibited at the two higher levels of ATA and dropped below that of controls at the 72-hour measurements. The drop in respiration at the higher concentrations after 48 hours coincided with rapid blade dehydration and the initiation of visual abscission. The IAA-treated disks were slightly above the controls in oxygen use but did not approach the highest levels of the amino triazole-treated blade tissue.

Results by Leinweber and Hall (69) using the blades, petioles and abscission zones of the four age classes of leaves described in a previous section, both from untreated and those treated with several defoliants, indicated that respiration in the abscission zone was one of the critical factors controlling foliar abscission. The results showed that abscission zone tissue

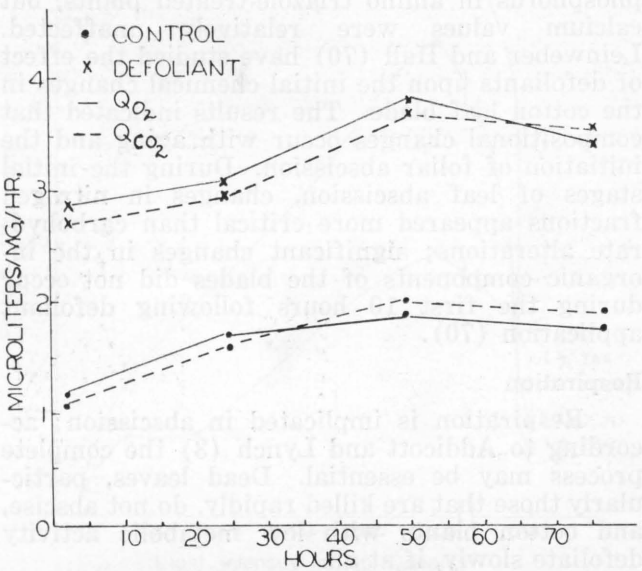


Figure 8. Comparison of respiratory rate of untreated and Shed-A-Leaf-treated leaf blade disks 80 hours following treatment. (After Hall and Lane, 1952.)

was the most reliable for detecting respiratory changes associated with the events of the abscission process.

Auxin, Growth Regulators and Theories

Although auxin (IAA) application to debladed petioles has been known to retard abscission for some time in other plants, it was not until 1950 that Hall demonstrated this in young cotton plants at first squaring. A detailed report of this was published in another outlet in 1952 (40). As reported in a previous section, Gawadi and Avery (37) noted that naphthoxyacetic acid applied to young debladed petioles did not retard abscission as it did in poinsettia but did inhibit formation of the abscission layer. Following their work with bean, Addicott and Lynch (1) and Addicott *et al.* (4) noted that IAA applied to the proximal side of the abscission zone accelerated abscission in cotyledonary explants of cotton. This has been confirmed by Hall (48) using the cotyledons of seedling cotton but not for single mature leaf pairs or intact debladed leaves on mature plants under natural conditions. In fact for mature tissue, application of IAA and NAA distally to the abscission zone accelerated abscission more than their proximal application. Carns (21) reported that the gradient of auxin across the cotton leaf abscission zone decreased as abscission approached.

Gawadi and Avery (37) and Hall (40) have demonstrated that ethylene chlorohydrin stimulates the rapid abscission of debladed cotyledonary and mature petioles. Jackson (59) reported that an aqueous solution of ethylene surrounding a portion of the petiole causes abscission of the treated leaf and also of leaves at nodes above and below the treated leaf. Hall (40) and Hall and Lane (42) showed that ethylene gas enclosed with cotton plants of different ages induced rapid abscission of all age classes of leaves. Based on their experiments with cotton and other plants, Gawadi and Avery (37) and Hall (40) proposed that the interaction of auxin and ethylene regulated foliar abscission. Using the permanganate method, Hall (41) reported production of ethylene by cotton leaves and the IAA-inhibition of ethylene production in mold preparations. Working with debladed petioles of *Coleus* and cotton, Hall (40) showed that auxins reduced or prevented the acceleration of abscission by ethylene and ethylene chlorohydrin and that two defoliants increased measurably the production of ethylene after blade application. Biale (14), Pratt (78) and Addicott and Lynch (3) have questioned the reliability of the permanganate method to measure ethylene production. Using a modification of the mercuric-perchlorate-manometric method, which Pratt (78) and Addicott and Lynch (3) have termed the "only universally approved method," Hall *et al.* (46) have found that both excised cotton leaves and intact cotton plants produce ethylene. Significant amounts of ethylene were not produced by healthy intact

TABLE 5. ETHYLENE PRODUCTION BY INTACT COTTON PLANTS AND DETACHED ORGANS[1]

Development stage and treatment	Length of experiment in hours	Total milliters $CH_2 = CH_2$ measured	Ml. $CH_2 = CH_2$ per kilogram fresh weight
	Intact plants		
Seedling	104	None	None
Young vegetative	94	0.22	0.099
Early reproductive	96	6.42	1.34
Fruiting	104	16.10	1.96
Mature-nonlethal defoliant treated	102	20.50	2.44
Mature-lethal defoliant treated	96	0.34	0.04
	Detached parts		
Mature green healthy leaves	102	0.14	0.13
Senescent chlorotic leaves	102	None	None
Mature unopened bolls	144	0.09	0.04

[1]All values at S.T.P. (standard temperature and pressure).

cotton plants until the flowering stage and production rose to a maximum in mature plants (Table 5). The results obtained have been compared to those obtained with the Young, Pratt, Biale (85) method and found to be in close agreement. Employing biological tests, Jackson (59) noted that an emanation, collected after removal of unsaturated hydrocarbons other than ethylene, was greater from cotton leaves treated with any of seven defoliants than from untreated leaves. This gas, when enclosed with other cotton plants, caused defoliation. Addicott and Lynch (3) stated that the pea test and the tomato epinastic test used by Jackson (59) are nonspecific and insufficient proof of the identity of ethylene. Regardless of the questionable direct proof that the gas was ethylene, Jackson (59) did show that the emanation was active in causing leaf abscission of untreated cotton plants and that the percentage of defoliation obtained by defoliant treatment of entire duplicate plants varied directly with the degree of the triple response in the pea test. Therefore, it is apparent that cotton leaves produce ethylene and that injury to the leaf stimulates further ethylene production. The critical experiment to demonstrate that ethylene is the direct cause of abscission and not a by-product of the abscission process remains to be conducted. Nevertheless, ethylene causes all of the known changes that occur in abscission and in spite of Addicott and Lynch's (3) conclusion that the ethylene part of the auxin-ethylene hypothesis is poorly supported, it is still premature to discard it as untenable.

Addicott *et al.* (5) concluded that auxin is the "principal endogenous regulator of abscission" and that consideration of all available information showed that a satisfactory explanation can be provided by an auxin gradient theory. The framework of this theory is presented in Figure 9. According to Addicott and Lynch (3), this theory is supported by (a) the lowering of the auxin gradient across the abscission zone previous to abscission and (b) the acceleration of abscission by proximal application of auxin. These workers visualize that applied auxin could accelerate abscission by lowering the effective distal concentration through competitive interaction with the endogenous auxin or if transported, by raising the proximal concentration. Also, they argue that augmenting the auxin supply distal to an abscission zone should help to maintain the flow of nutrients to the leaf or petiole and thus indirectly retard abscission. Conversely, application of auxin proximal to the abscission zone should accelerate the preabscission withdrawal of nutrients and thus indirectly accelerate abscission. Addicott and Lynch (3) state that the stem tissue proximal to the abscission zone is characteristically low in auxin, yet most basic discussions on auxin physiology note that the apical meristem is the primary site of auxin production in a plant and that auxin moves basipetally in the stem and therefore, if not inactivated, should reach the proximal side of the abscission zone in the highest amounts. If this is the case, then young leaves should abscise as they form, due to their proximity to the apical meristem. Hall and Liverman (45) found that the growing point region had no significant effect on the speed or percentage abscission in either young seedlings or mature plants. Neither does the auxin gradient theory explain the findings of Galston and Dalberg (35) that IAA-oxidase is an adaptative enzyme, with highest activity in mature tissue. It should be noted that the concentrations of exogenous auxin normally used to cause stimulation of abscission when applied proximally are in excess of physiological

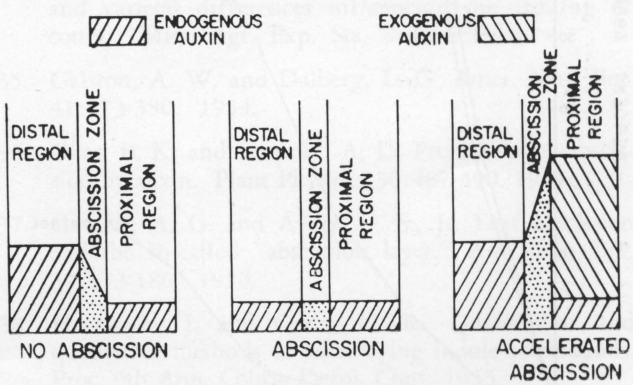


Figure 9. Graphic representation of the auxin gradient theory of abscission.

TABLE 6. EFFECTS OF PROXIMAL AND DISTAL APPLICATIONS OF AUXINS UPON ABSCISSION OF 21-DAY-OLD COTTON SEEDLING EXPLANTS WITH EACH TREATMENT THE AVERAGE OF 192 SEEDLINGS

Treatment	Percent abscission, 3 days		Percent abscission, 7 days	
	NAA	IAA	NAA	IAA
Control—lanolin proximal and distal	15	3	41	40
1 p.p.m. distal—lanolin proximal	8	3	77	53
10 p.p.m. distal—lanolin proximal	0	0	31	63
100 p.p.m. distal—lanolin proximal	0	0	15	38
1 p.p.m. proximal—lanolin distal	28	10	78	83
10 p.p.m. proximal—lanolin distal	48	14	89	82
100 p.p.m. proximal—lanolin distal	0	15	51	84
1 p.p.m. proximal—1 p.p.m. distal	7	6	78	68
1 p.p.m. proximal—10 p.p.m. distal	0	1	43	37
10 p.p.m. proximal—1 p.p.m. distal	7	2	68	60
10 p.p.m. proximal—100 p.p.m. distal	0	1	21	33
100 p.p.m. proximal—10 p.p.m. distal	0	0	36	32

concentrations and this effect may cause abnormal reactions. Experiments of Hall and Herrero (47) showed that as long as ethylene chlorohydrin is applied distally, auxin applied proximally is essentially without effect. The results of these experiments showed some evidence to support the auxin gradient theory in the abscission of cotyledons in seedlings but little evidence existed in mature plants.

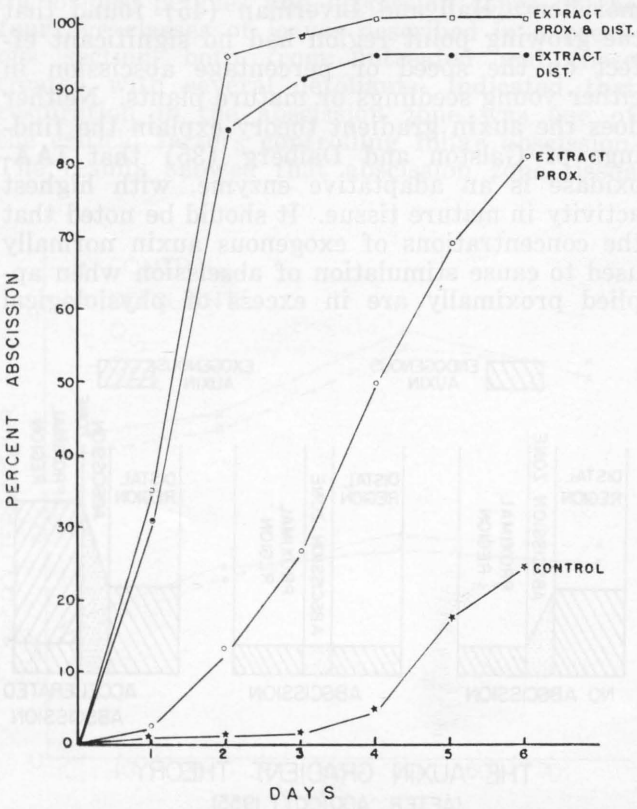


Figure 10. The effect of an ether-soluble extract from abscising cotton leaf abscission zones upon abscission of cotton cotyledonary explants when applied as indicated.

Gaur and Leopold (36), studying leaf abscission in *Coleus* and bean, concluded that differences in effects of proximal and distal applications of NAA are more quantitative than qualitative. They found that NAA could both inhibit and promote abscission and stated that the controlling factor is the concentration and not the auxin gradient. Herrero and Hall (57) repeated the experiments of Gaur and Leopold (36) on the concentration effects of NAA using cotton cotyledonary node explants (Table 6). It was found that both the concentration of NAA and its site of application were important in regulating abscission; whenever the distal concentration was sufficiently high in relation to the proximal application, inhibition of abscission resulted. Essentially the same results were obtained using IAA (Table 6). The lack of a pronounced promoting or photoreversal reaction to red-far red-auxin treatments as found for other morphogenetic responses, led Hall and Liverman (45) to conclude that abscission is not solely an auxin-mediated response.

In 1955, Osborne (77) reported finding a diffusible abscission-promoting factor in mature or senescent leaves of species other than cotton. Attempts by Herrero and Hall (57) to isolate the factor from abscising cotton petiole pulvini by diffusion into agar or aqueous extraction failed to demonstrate any acceleration of abscission in cotton cotyledonary explants. The ethanol or ether extract, however, gave marked promotion of abscission when applied either distally or proximally to the abscission zone (Figure 10). The active fraction was heat stable and inhibitory to *Avena* section growth. A negative Salkowski reaction and other tests indicated that it was not an indole auxin-type compound.

Experiments have shown that other regulators, synthetic auxins, anti-auxins or auxin competitors, affect defoliation. Hall *et al.* (43) found that maleic hydrazide applied alone to intact leaves had little effect on defoliation, but if applied prior to or with known defoliants it accelerated defoliation. Several of the synthetic auxins applied alone or with a defoliant reduced leaf-fall; however, some of the synthetic auxins applied 3 weeks before the defoliant, slightly stimulated defoliation, possibly by competitive inhibition with native auxin. Transcinnamic acid applied to debladed petioles is an effective defoliant (40) yet applications to intact blades are ineffectual. All of these observations suggest that the basic cause of leaf abscission in cotton cannot be explained on the basis of auxin alone, but other factors are of equal importance.

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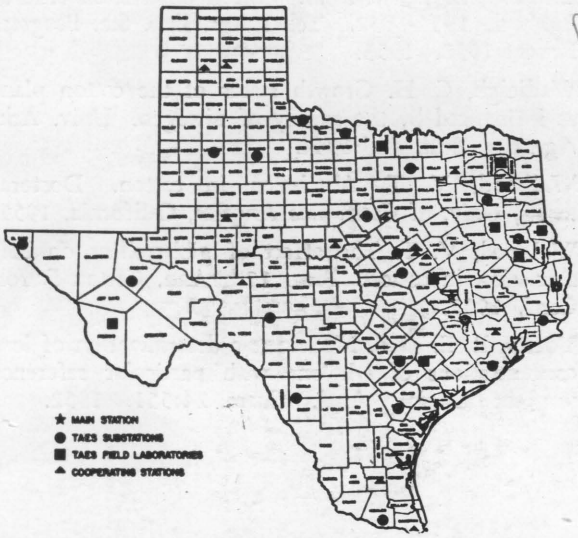

Location of field research units of the Texas Agricultural Experiment Station and cooperating agencies

State-wide Research

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The Texas Agricultural Experiment Station is the public agricultural research agency of the State of Texas, and is one of ten parts of the Texas A&M College System

ORGANIZATION

IN THE MAIN STATION, with headquarters at College Station, are 16 subject-matter departments, 2 service departments, 3 regulatory services and the administrative staff. Located out in the major agricultural areas of Texas are 21 substations and 9 field laboratories. In addition, there are 14 cooperating stations owned by other agencies. Cooperating agencies include the Texas Forest Service, Game and Fish Commission of Texas, Texas Prison System, U. S. Department of Agriculture, University of Texas, Texas Technological College, Texas College of Arts and Industries and the King Ranch. Some experiments are conducted on farms and ranches and in rural homes.

OPERATION

THE TEXAS STATION is conducting about 400 active research projects, grouped in 25 programs, which include all phases of agriculture in Texas. Among these are:

Conservation and improvement of soil
Conservation and use of water
Grasses and legumes
Grain crops
Cotton and other fiber crops
Vegetable crops
Citrus and other subtropical fruits
Fruits and nuts
Oil seed crops
Ornamental plants
Brush and weeds
Insects
Beef cattle
Dairy cattle
Sheep and goats
Swine
Chickens and turkeys
Animal diseases and parasites
Fish and game
Farm and ranch engineering
Farm and ranch business
Marketing agricultural products
Rural home economics
Rural agricultural economics
Plant diseases

Two additional programs are maintenance and upkeep, and central services.

Research results are carried to Texas farmers, ranchmen and homemakers by county agents and specialists of the Texas Agricultural Extension Service

AGRICULTURAL RESEARCH seeks the WHATS, the WHYS, the WHENS, the WHERES and the HOWS of hundreds of problems which confront operators of farms and ranches, and the many industries depending on or serving agriculture. Workers of the Main Station and the field units of the Texas Agricultural Experiment Station seek diligently to find solutions to these problems.

Today's Research Is Tomorrow's Progress